Systematic & Applied Acarology (2006) 11, 141–157. ISSN 1362-1971

Biology and predation of the Japanese strain of *Neoseiulus californicus* (McGregor) (Acari: Phytoseiidae)

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Abstract

The life history characteristics and predation of the Japanese *Neoseiulus californicus* (McGregor) strain on the two-spotted spider mite, *Tetranychus urticae* Koch, were studied in the laboratory under 60–70% RH and 16L: 8D conditions. Developmental time from egg to adult emergence decreased when temperature increased. Total development period of immature stages was longest at 15°C and shortest at 35°C for both male and female. Sex ratio favored females and temperature did not exert a critical effect on sex determination. The total degree-days required from egg to adult female were 71.43 degree-days with thermal constant of 10.64°C. At 25°C, female laid a total of 34.73 eggs during 17.91 days of oviposition period. The net reproductive rate (R_o) was highest at 25°C (22.92 females/female) and lowest at 30°C (16.74 females/female). The mean generation time (T) decreased from 20.61 to 16.79 days with increasing temperature up to 30°C. The intrinsic rate of natural increase (r_m) ranged from 0.162 to 0.285, and was maximal at 25°C. A gravid *N. californicus* female consumed more eggs, larvae and nymphs than adult male or female of *T. urticae*. As *T. urticae* density increased, prey consumption likewise increased. However, increasing the number of adult male or female preys did not increase the number of eggs laid by a female predator. The results were used to assess the effectiveness of the Japanese *N. californicus* strain as an important biological control agent against *T. urticae.*

Key words: development, life history, *Neoseiulus californicus*, predation, spider mite, *Tetranychus urticae*

Introduction

Neoseiulus californicus (McGregor) (Acari: Phytoseiidae), is a predatory mite widely distributed (McMurtry 1977; McMurtry & Croft 1997). It has been used for the control of spider mites in field and greenhouse horticultural crops in North and South America and Europe (Swirski *et al*. 1970; Oatman *et al*. 1977; Picket & Gilstrap 1986a & b; Castagnoli & Simoni 1991; Raworth *et al*. 1994; McMurtry & Croft 1997; Jolly 2000). Its versatility as a predator has been noteworthy not only because it can prey on almost all stages of the two-spotted spider mites, *Tetranychus urticae* Koch (Acari: Tetranychidae) but also it has the ability to prey on other tetranychid species, as well as on other pest mites, other insects and can even survive on pollen (Swirski *et al*. 1970; McMurtry 1977; Friese & Gilstrap 1982; Castagnoli & Liguori 1991; McMurtry & Croft 1997; Croft *et al.* 1998). Their use is increasingly gaining importance because of the pressure on growers to find alternatives to chemical pesticides (Coping 2001).

Neoseiulus californicus is found naturally in Japan and was first recorded in 1963 from pear trees and weeds (Ehara 1964). Since then, several studies were conducted on the distribution and taxonomy of this indigenous species (Ehara 1964; Ehara & Amano 2004; Amano 1999 & 2001). Similarly, many reports on the general biology and predation ability of *N. californicus* strains from Europe and North and South America have been published (Swirski *et al*. 1970; Ma & Laing 1973;

Mesa *et al*. 1990; Castagnoli & Simoni 1991; Raworth *et al*. 1994; McMurtry & Croft 1997; Rencken & Pringle 1998; Blumel & Walzer 2002; Hart *et al*. 2002). However, few literatures exist about the biological traits of the Japanese *N. californicus* strain.

Toyoshima and Hinomoto (2004) assessed the reproductive characteristics and predation of the Japanese *N. californicus* strain on *T. urticae* females and compared it with the commercial strain at 20°C. Gotoh *et al*. (2004) determined the effect of five constant temperatures on its life history parameters using a diet of eggs of the red form of *T. urticae*. However, no details about the reproductive rate and predation of the Japanese strain at different prey stages and densities were given in these studies. For these reasons, more experimental approaches to study the processes of predation by this phytoseiid mite were deemed essential to fully understand the prey-predator interactions. Hence, the present study was undertaken as a contribution to this field. The paper describes the influence of temperature on reproductive parameters of the Japanese *N. californicus* strain using the green form of *T. urticae* as prey as well as assess its predation ability at various prey stages and densities under laboratory conditions.

Materials and methods

Colony source and stock culture

A laboratory colony of a Japanese strain of *N. californicus* was initiated at Kobe University from the original collections (Ichihara, Chiba 1995) of Dr. Hiroshi Amano. The predators were mass-reared with the green form of *T. urticae* as prey, following the detached leaf method of Amano & Chant (1977). The stock culture of *N. californicus* was maintained in an environmental chamber that was controlled at 25ºC, 60–70% relative humidity (RH) and 16 hours light (L): 8 hours dark (D) conditions. *T. urticae* populations were maintained on kidney bean plants *Phaseolus vulgaris* L., kept separately in an environmental chamber with the same conditions as that of the predatory mites.

Development of immature stages

Developmental time of *N. californicus* from egg to adult emergence was examined at 15, 20, 25, 30 and 35ºC. Ovipositing females were kept on excised kidney bean leaf with sufficient composite stages of *T. urticae* as prey. Newly laid eggs were removed and reared individually on excised kidney bean leaf as mentioned before. Observations were made at intervals of 12 hours and every molt was recorded until the sample mites emerged into adults. The sex of the emerging adult was likewise recorded. All stages of *T. urticae* were provided abundantly, and additional preys were supplied whenever necessary. Sample mites that developed into males were discontinued wherein those that developed into females were used for the fecundity studies.

Data were analyzed using SigmaStat3.1 for Windows (Systat Software Inc., 2004). Differences in developmental time and longevity at various temperatures were analyzed with the general linear model procedure. Multiple comparisons of treatment means were done using Holm-Sidak method. Simple linear regression was performed and was used to provide estimates of the threshold temperature (*t*, ºC) and the time-to-adult (K, degree-days or DD) requirements for this species. The Standard Error (S.E.) of the lower temperature threshold (*t*) and the sum of heat units (K) were estimated according to Campbell *et al*. (1974). Approximately, the S.E. of *t* was:

$$\bar{y}/b \sqrt{s^2/N\bar{y} + [\text{S.E. of b/b}]^2}$$

where s is the residual mean square of y and $\bar{y}$ is the sample mean. The S.E. of *K* was approximated by: (S.E. of b) /b^2. Intersexual differences were analyzed using Mann-Whitney *U*-test.

Female survival and reproduction

The fecundity of *N. californicus* was determined at 20, 25 and 30ºC. From the above study, before the final molt of the female deutonymph, one adult male was provided and was ensured to mate once. The male was then removed and observations were made at intervals of 6 hours until the first egg was laid. Thereafter, the number of eggs laid were recorded every 24 hours until the ovipositing female died. All the eggs that were laid were removed and transferred individually to new excised bean leaf and were reared until adult to record the sex of the resulting F1 progeny. Oviposition period, pre- and post-oviposition period was also calculated.

The intrinsic rate of natural increase (r_m) at 20, 25 and 30ºC was estimated according to the equation given by Birch (1948). The following life history parameters were determined after Hulting *et al*. (1990): net reproductive rate (R_o), mean generation time (T), and finite rate of increase (λ). Longevity and fecundity data were analyzed with Mann-Whitney *U*-test or Kruskal-Wallis test. Multiple comparisons of means were done by Holm-Sidak method.

Predation ability

To determine the predation rate of *N. californicus*, female deutonymphs were transferred individually to an excised bean leaf and was allowed to mate with a one-day old male for 24 hours. After mating, the male was removed and the female remained confined on the detached leaf and was provided with either egg, larva, nymph, male or female adult of *T. urticae* at the density of 5, 10, 20, 30, 40, and 50, respectively. The number of prey consumed and eggs laid per sample phytoseiid mite was recorded every 24 hours. Consumed preys and eggs laid by the sample phytoseiid mite were removed every observation period and the number of prey was brought back to the original count by adding new ones. The experiment was replicated five times and was conducted for 7 consecutive days in an environmental chamber with 25ºC, 60–70% RH and 16L: 8D conditions. Data were analyzed using the general linear model and Holm-Sidak Method was employed to separate the differences in treatment means. The data from the first day were excluded from the final analysis to dismiss the possibility of unusual response of the sample phytoseiid mites to an abrupt change in prey stage and density.

Results

The developmental time of immature stages of Japanese *N. californicus* strain is shown in Table 1. Temperature affected the developmental time of all immature stages. Developmental time decreased significantly with increasing temperature up to 35ºC ($P<0.001$). Total developmental time of immature stages was longest at 15ºC and averaged at 19.75 days for males and 21.71 days for females. It was shortest at 35ºC with an average of 3.41 days for males and 3.78 days for females. The total developmental time did not significantly differ between sexes at any of the temperatures tested ($P> 0.05$, Mann-Whitney *U*-test).

Table 2 shows the simple linear regression analysis applied to the developmental rate and temperature from 15 to 30ºC. The egg stage has the highest development threshold (11.77ºC) in females, while the deutonymph stage has the highest development threshold (12.97ºC) for males. The total degree-days required from egg to adult female (71.43DD) were similar to that from egg to adult male (72.46DD). Using the degree-days per generation values obtained from the developmental threshold calculations from egg to adult female in combination with mean daily temperatures from 1994 to 2004 supplied by the meteorological station of the university, it was estimated that at least six generations per year are possible in the western part of Japan. Up to 10 generations maybe feasible in the summer season.

TABLE 1. Developmental time (in days) of immature stages of *N. californicus* at five constant temperatures under 16L: 8D conditions.[a]

Temperature (ºC)	Sex	n [b]	Egg	Larva	Protonymph	Deutonymph	Total	Intersexual difference[c] (P)
15	Male	8	6.94 ± 0.17[a]	2.87 ± 0.08[a]	3.87 ± 0.20[a]	6.06 ± 0.25[a]	19.75 ± 0.25[a]	0.059
	Female	14	6.07 ± 0.20[a]	2.71 ± 0.10[a]	5.68 ± 0.20[a]	7.25 ± 0.30[a]	21.71 ± 0.25[a]	
20	Male	9	2.17 ± 0.08[b]	0.94 ± 0.10[b]	1.44 ± 0.10[b]	2.11 ± 0.25[b]	6.67 ± 0.30[b]	0.978
	Female	19	2.24 ± 0.05[b]	0.97 ± 0.06[b]	1.71 ± 0.10[b]	1.81 ± 0.11[b]	6.74 ± 0.15[b]	
25	Male	13	1.42 ± 0.05[c]	0.77 ± 0.07[b]	1.07 ± 0.05[bc]	1.35 ± 0.10[c]	4.62 ± 0.18[c]	0.233
	Female	25	1.60 ± 0.04[c]	0.78 ± 0.05[c]	1.44 ± 0.07[bc]	1.24 ± 0.07[c]	5.06 ± 0.13[c]	
30	Male	10	2.20 ± 0.08[d]	0.55 ± 0.05[c]	1.00 ± 0.12[bc]	0.85 ± 0.07[c]	3.85 ± 0.08[d]	0.661
	Female	15	1.23 ± 0.06[d]	0.53 ± 0.03[d]	1.10 ± 0.05[c]	1.03 ± 0.05[c]	3.87 ± 0.09[d]	
35	Male	16	1.03 ± 0.09[d]	0.50 ± 0[c]	0.87 ± 0.08[c]	1.00 ± 0.06[c]	3.41 ± 0.15[d]	0.418
	Female	18	1.14 ± 0.07[d]	0.50 ± 0[c]	1.11 ± 0.09[c]	1.03 ± 0.10[c]	3.78 ± 0.10[d]	

[a]All values are means ±SEM. Means for each stage of the same sex in the same column followed by different letters were significantly different at $P<0.05$ Holm-Sidak Method.
[b]n = number of samples.
[c]Intersexual difference based on total developmental time was analyzed using Mann-Whitney *U*-test.

TABLE 2. Linear regression analysis of developmental rate and temperature, and estimated lower developmental threshold and thermal constant in *N. californicus* under 16L: 8D conditions.

Sex/Stage	Regression Equation	r^2	Lower developmental threshold (t_o, ºC)	Thermal constant (K, degree-days, DD)
Female				
Egg	$y = -0.605 + 0.0514x$	0.93 ($P<0.001$)	11.77±0.16	19.45±0.62
Larva	$y = -1.032 + 0.1000x$	0.97 ($P<0.01$)	10.32±0.66	10.00±1.16
Protonymph	$y = -0.452 + 0.0479x$	0.92 ($P<0.01$)	9.44±0.89	20.88±4.29
Deutonymph	$y = -0.643 + 0.0588x$	0.92 ($P<0.01$)	10.94±1.22	17.01±3.55
Egg-adult	$y = -0.149 + 0.0140x$	0.97 ($P<0.01$)	10.64±0.71	71.43±9.28
Male				
Egg	$y = -0.596 + 0.0510x$	0.93 ($P<0.001$)	11.69±0.24	19.61±0.87
Larva	$y = -0.993 + 0.0985x$	0.95 ($P<0.01$)	10.08±0.94	10.15±1.67
Protonymph	$y = -0.580 + 0.0606x$	0.97 ($P<0.01$)	9.57±0.70	16.50±2.03
Deutonymph	$y = -0.951 + 0.0733x$	0.98 ($P<0.001$)	12.97±0.52	13.64±1.21
Egg-adult	$y = -0.139 + 0.0138x$	0.95 ($P<0.01$)	10.07±0.89	72.46±10.34

Simple linear regression analysis was applied to the developmental data within 15–30ºC.
Mean ± S.E.
Standard errors were estimated according to the equations given by Campbell *et al*. 1974.

Female survival and fecundity

The duration and rate of reproduction of the Japanese *N. californicus* strain are shown in Table 3. The average daily oviposition per female was lowest at 20ºC. The total number of eggs laid per female was higher at 25ºC than at 30 and 20ºC. Preoviposition period, postoviposition period, oviposition period and total adult longevity became shorter as temperature increased.

TABLE 3. Duration and rate of reproduction of *N. californicus* adult females at three constant temperatures under 16L: 8D conditions.

Parameter	Temperature (°C)			χ^2 – value
	20 (n=10)	25 (n=22)	30 (n=10)	
Pre-oviposition period	2.20±0.13[a]	1.68±0.13[a]	1.10±0.10[b]	16.80***
Oviposition period	16.70±1.20[ab]	17.91±1.00[a]	11.70±1.30[b]	60.89***
Postoviposition period	17.60±2.40[a]	10.18 0.88[ab]	7.70±0.95[b]	47.44**
Total no. of eggs/female	25.80±4.50[a]	34.73±2.23[b]	27.90±3.40[c]	78.91***
Average no. of eggs/female/day	1.54±0.36[a]	1.94±0.24[b]	2.34±0.28[c]	76.67**
Total adult longevity	36.20±0.20[a]	29.27±2.40[b]	21.60±0.16[c]	69.60***

Pre-oviposition, oviposition, postoviposition periods and total adult longevity measured in days.
n=number of samples.
Means ± S.E.M. in a row followed by different letters were significantly different at $P<0.05$ Holm-Sidak Method.
$^{**}P < 0.01$.
$^{***}P < 0.001$.

Age-specific survival and age-specific fecundity measured in days at 20, 25 and 30ºC are presented in Fig. 1. At all temperatures tested, little mortality occurred until age 10. The sharp decline in the survival curve occurred at ages 15–18 at 20 and 30ºC and at ages 21–28 at 25ºC. Fifty percent of females survived between ages 20–23 at 20 and 25ºC and between ages 15–19 at 30ºC. At 20, 25 and 30ºC, females started to die at ages 40, 31, and 22, respectively.

At 20ºC, oviposition generally began at age 5, while at 25 and 30ºC, at ages 3 and 2, respectively (Fig. 1). Daily oviposition rates peaked between ages 11–13 at 25 and 30ºC. However, at 20ºC, the distinctive trend in daily oviposition was not observed. At 25 and 30ºC, daily oviposition rates declined gradually after reaching their peaks. The daily reproductive rate at 30ºC declined earlier than at 25 and 20ºC (Fig. 1).

The estimated values of life table parameters for *N. californicus* are listed in Table 4. The mean generation time (T, in days) decreased when temperature increased. The net reproductive rate (R_o) was higher at 25ºC than at 20 and 30ºC. The intrinsic rate of natural increase (r_m) was highest at 30ºC (0.285) followed by 25ºC (0.209) and 20ºC (0.162). The finite rate of increase (λ) and r_m increased with temperature.

TABLE 4. Life table parameters of *N. californicus* at three constant temperatures under 16L: 8D conditions.

Temperature (°C)	Mean generation time (T, days)	Net reproductive rate (R_o)	Intrinsic rate of natural increase (r_m/day)	Finite rate of increase (λ)	Sex ratio (F:M)[a]
20 (n=10)	20.61	18.09	0.162	1.18	2.1:1
25 (n=22)	17.55	22.92	0.209	1.23	1.9:1
30 (n=10)	16.79	16.74	0.285	1.25	1.5:1

n=number of samples.
[a]Female and male proportion of the F1 progeny.

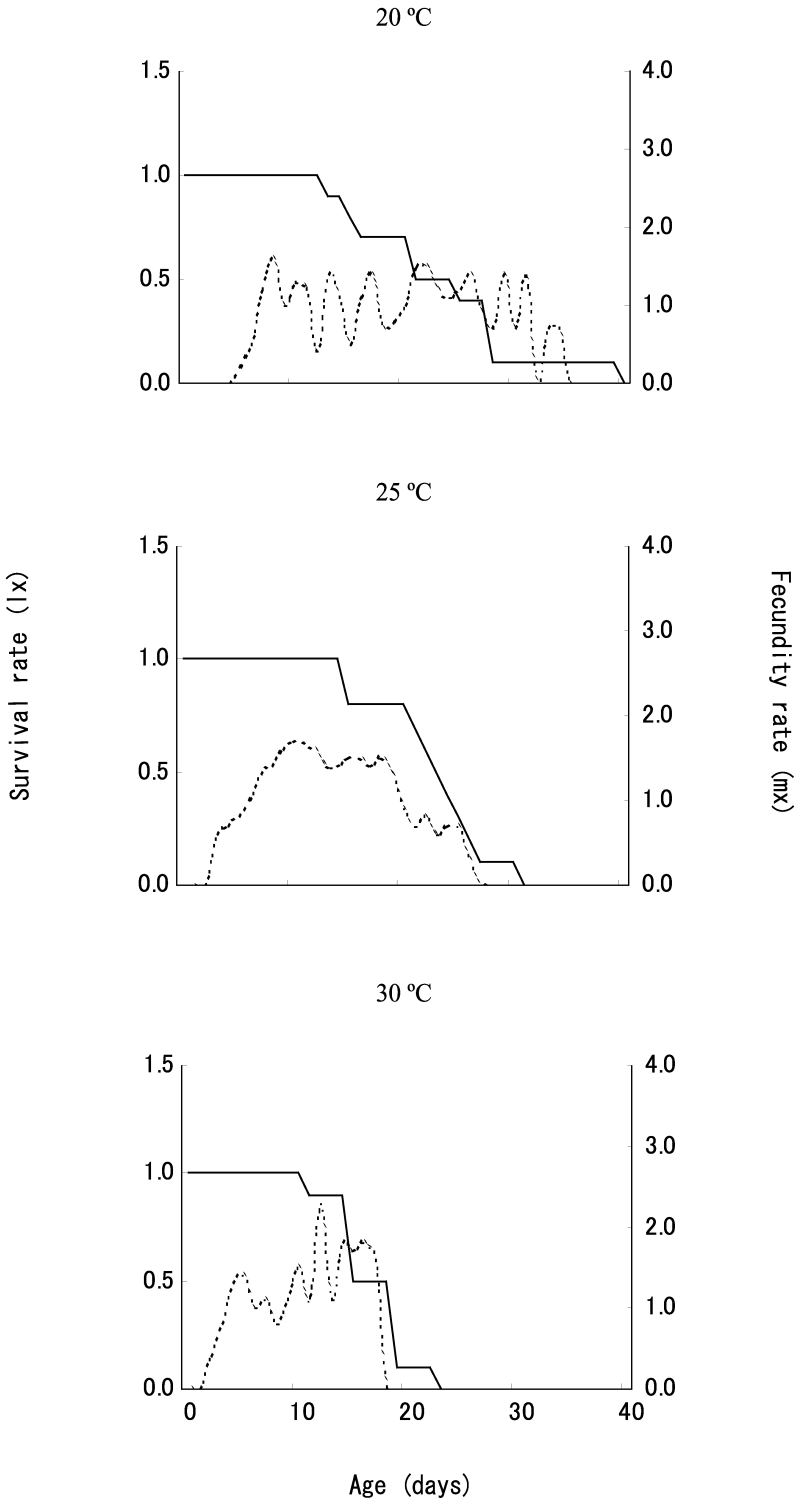

FIGURE 1. Age-specific survival (l_x)(straight line) and age-specific fecundity (m_x) (dotted line) of *N. californicus* females at 20, 25 and 30 °C under 16L: 8D conditions.

The sex ratio of the F1 progeny was more than 1.0 in favor of females at 20, 25 and 30ºC (Table 4). While temperature increased and female ratio slightly decreased; the temperature effect was not significant (P>0.05, Mann-Whitney U-test).

Prey consumption

The average daily number of prey consumed by the Japanese *N. californicus* gravid females at various prey stages and densities of *T. urticae* is exhibited in Table 5. Consumption of egg, juvenile and adult male stages of *T. urticae* was significant (P<0.001, Friedman test). The average number of prey consumed by *N. californicus* females feeding on eggs, larvae or nymphs of *T. urticae* increased at an accelerated rate when 5 to 30 preys were provided. Regardless of prey density, eggs, larvae and nymphs were preferred over adult male or female preys. The highest number of eggs, larvae and nymphs consumed by one gravid female per day was 20.91, 22.46 and 12.57, whereas, predation at these levels ranged from 1–40, 2–35, and 1–19, respectively. While predation at different densities of adult male was significant (Table 5), increasing the number of adult female preys had no effect on the rate of predation of *N. californicus* (P>0.05). The highest number of adult male and female prey consumed by a female predator was 9.22 and 2.51, respectively.

An increase in density of eggs, larvae and nymphs eventually resulted in a higher predation rate (Fig. 2). However, predation rate started to level off at 40–50 prey densities. More so, predation rate remained low when either adult male (3.46–9.22 adult male prey/female/day) or female (0.97–2.51 adult female prey/female/day) were offered as preys.

TABLE 5. Average daily number of prey consumed by *N. californicus* gravid female at various stages and densities of *T. urticae* under 25ºC,16L: 8D conditions.

Prey density	Prey Stage Egg	Larva	Nymph	Adult male	Adult female
5	2.17 ±0.24[a]	4.53±0.14[a]	3.91±0.18[a]	3.46±0.16[a]	0.97±0.12[a]
	R=1–5	R=2–5	R=1–5	R=2–5	R=0–2
10	4.23±0.25[a]	5.80±0.20[a]	6.17±0.42[a]	4.51±0.44[a]	1.65±0.25[ab]
	R=2–7	R=3–8	R=2–10	R=1–8	R=0–6
20	12.83±0.79[b]	12.94±0.48[b]	9.14±0.80[bc]	6.40±0.37[ab]	2.43±0.29[b]
	R= 4–20	R=3–17	R=2–18	R=2–9	R=0–7
30	16.06±1.10[bc]	16.33±0.77[b]	8.51±0.35[bc]	8.51±0.58[b]	2.00±0.14[ab]
	R=3–25	R=5–25	R=6–13	R=2–16	R=1–3
40	17.49±1.07[cd]	22.46±0.75[c]	10.77±0.55[cd]	7.83±0.66[bc]	1.91±0.16[ab]
	R=6–32	R=8–29	R=3–19	R=3–16	R=1–4
50	20.91±1.61[d]	21.06±1.13[c]	12.57±0.66[d]	9.22±0.69[bc]	2.51±0.26[ab]
	R=10–40	R=10–35	R=1–18	R=3–21	R=0–4
Regression Equation	y=-1.69+2.25x (P<0.001)	y=-4.93+2.18x (P<0.001)	y=-19.59+5.33x (P<0.001)	y=-21.84+7.16x (P<0.01)	y=-17.04+22.40x ns[a]
r^2	0.92	0.95	0.91	0.89	0.52

Mean±S.E.M followed by different letters were significantly different at $P<0.05$ Holm-Sidak Method.
x^2=483.74, Friedman test.
R= range.
[a]Not significant at P>0.05.

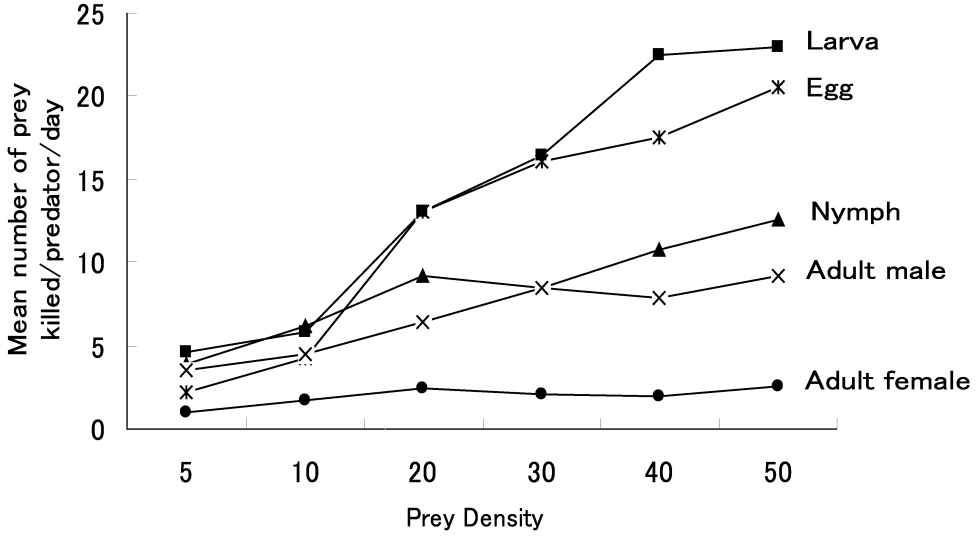

FIGURE 2. Average daily prey consumption of *N. californicus* females at various stages and densities *T. urticae* at 25°C, 16L: 8D conditions.

The average oviposition of the Japanese *N. californicus* strain in relation to prey consumption is shown in Table 6. Oviposition rate was significant only when preying on juvenile stages of *T. urticae* ($P<0.01$, Friedman test). The number of eggs laid by a female fed with eggs, larvae or nymphs of *T. urticae* increased slightly with increasing prey density. As a result, the maximum number of eggs oviposited by a female predator was 1.91, 1.69 and 1.71 when 50 eggs, larvae, or nymphs were provided, respectively. However, increasing the number of adult male or female of *T. urticae* had no effect on the daily number of eggs deposited by a female predator ($P>0.05$). The highest oviposition rate was 0.83 eggs/female/day when fed with adult male preys and 1.17 eggs/female/day when fed with adult female preys. The daily oviposition rate was high when eggs, larvae and nymphs were offered as preys (Fig. 3). However, oviposition rate remained low even when offered with high density of adult male (0.11–0.83 egg/day/female) or female (0.40–1.17egg/day/female). Although predation on adult male was statistically significant, it had no effect on the oviposition rate. Even when the adult male or female prey density was increased, oviposition rate did not increase (Fig. 3).

Discussion

Phytoseiid mites are known to have shorter developmental times than their spider mite prey, which has the shortest developmental time among the tetranychids (Sabelis 1985b; Walter & Proctor 1999). The Japanese *N. californicus* strain used in this study appears to share the same short developmental time along with the other phytoseiid mites important for biological control. The developmental time of the Japanese *N. californicus* strain at 20–30ºC is almost similar with that of other *Amblyseius* species (Table 7). However, among the *N. californicus* so far studied, this Japanese strain had the longest developmental time (20.7 days) at 15ºC together with *A. cucumeris* (Oudemans) (20.0 days) (Zhang *et al.* 2003) (Table 7). This might be due to the differences in foods supplied as well as local strains used. The development of *A. womersleyi* (Schicha) also changed when fed with different

foods such as *Tetranychus kanzawai* Kishida eggs (Shih & Shieh 1979; Kim *et al*. 1996) and *T. kanzawai* nymphs (Lo 1984). Also, the variations in the developmental time of *N. californicus* can be attributed to the different observation intervals in the different studies. Most of these experiments used 6–12 h intervals, which might contribute to the possible inflation of immature duration time. In the present study, immature development time was monitored strictly in 12h intervals. But overall, the findings suggest that the Japanese *N. californicus* strain, like other predatory mites, can develop in a wide range of temperatures.

TABLE 6. Average daily number of egg deposited by a *N. californicus* gravid female at various stages and densities of *T. urticae* under 25ºC, 16L: 8D conditions.

Prey density	Prey Stage				
	Egg	Larva	Nymph	Adult male	Adult female
5	0.57±0.11^{ab}	0.51±0.09^{a}	0.51±0.08^{a}	0.34±0.18	0.60±0.17
	R=0–2	R=0–2	R=0–1	R=0–2	R=0–3
10	0.66±0.08^{b}	0.80±0.13^{ab}	0.80±0.12^{ab}	0.11±0.05	0.80±0.23
	R=0–1	R=0–2	R=0–2	R=0–2	R=0–5
20	0.86±0.10^{ab}	1.29±0.10^{ab}	1.11±0.16^{ab}	0.74±0.14	1.17±0.19
	R=0–2	R=0–2	R=0–3	R=0–2	R=0–3
30	1.43±0.18^{bc}	1.37±0.77^{b}	1.63±0.25^{b}	0.80±0.14	0.77±0.16
	R=0–3	R=0–3	R=0–4	R=0–2	R=0–3
40	1.34±0.20^{bc}	1.65±0.15^{b}	1.40±0.15^{b}	0.83±0.19	0.63±0.16
	R=0–3	R=0–3	R=0–4	R=0–3	R=0–3
50	1.91±0.18^{bc}	1.69±0.15^{b}	1.71±0.19^{b}	0.80±0.17	0.40±0.15
	R=0–3	R=0–3	R=0–4	R=0–3	R=0–3
Regression Equation	y=-10.62+32.30x (P<0.01)	y=-17.05+35.18x (P<0.01)	=-14.76+34.02x (P<0.01)	y=-2.24+46.79x ns^{a}	y=47.90-30.28x ns^{a}
r^2	0.93	0.90	0.85	0.64	0.20

Mean±S.E.M followed by the different letters were significantly different at $P<0.05$ Holm-Sidak Method.
$x^2$105.73, Friedman test.
R= range.
[a]Not significant at $P>0.05$.

The lower threshold temperature (t) of the Japanese *N. californicus* strain was close to that of the other *Amblyseius* species (Table 7). However, the thermal constant (K) of the Japanese strain is longer than with the same strain used by Gotoh *et al*. (2004) but shorter than that of the Italian, African, and American strains (Table 7). This was expected since populations of a given species may vary in their thermal constants from place to place (Campbell *et al*. 1974). The aphid parasite *Diaeretiella rapae* M`Intosh reared in constant temperature but in different locations (Canada, U.S. and the Netherlands) showed almost the same threshold temperature but variable thermal constants (Campbell *et al*. 1974). Thus the same species have varying reactions to similar conditions. Since K is an important measure in determining the turnover of successive generation, the number of generations of *N. californicus* will differ between and among strains according to the prevailing conditions in a given location.

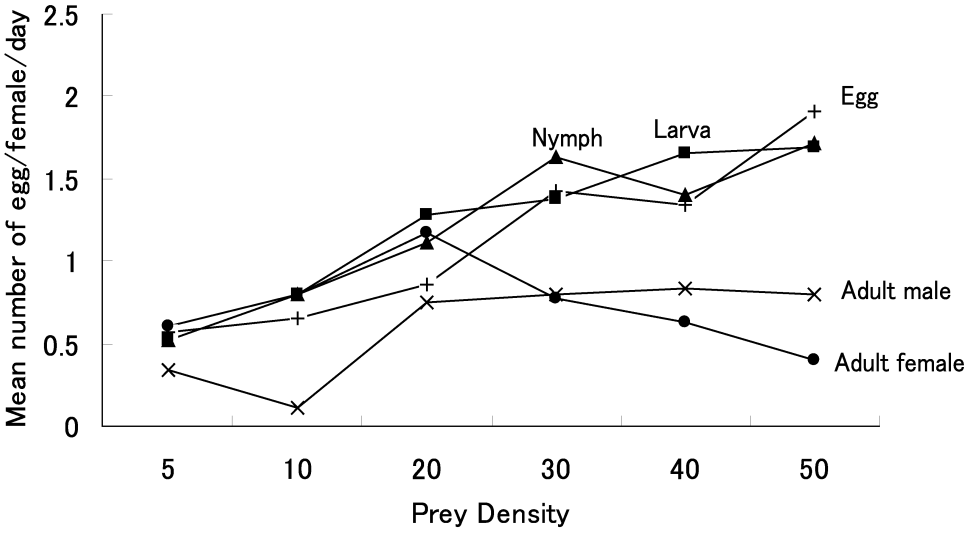

FIGURE 3. Average daily oviposition of *N. californicus* females at various stages and densities *T. urticae* at 25°C, 16L: 8D conditions.

TABLE 7. Some developmental parameters for some *Amblyseius* species at temperatures ranging from 15–30ºC.[a]

Species	Prey[b]	t_o (ºC)	K (DD)	Developmental period (in days) 15± 2ºC	20±2ºC	25ºC	30± 2ºC	Reference
A. andersoni	*T. urticae* (G)	10.8	93.0	-	10.6[c]	6.6[c]	4.8[c]	Genini *et al*. (1991)
A. californicus	*T. urticae* (G), E	-	-	11.4[c]	-	5.0[c]	3.9[c]	Ma & Laing (1973)
A. californicus	*T. urticae*, AS	9.0	90.0	11.5[c]	7.2[c]	5.8[c]	4.4[c]	Castagnoli & Simoni (1991)
A. californicus	*T. urticae* ,AS	8.3[c]	100.1[c]	-	9.2	5.7	4.8	Rencken & Pringle (1998)
A. californicus	*T. urticae* (G), E	9.9	123.5	-	8.1	-	-	Hart *et al*. (2002)
A. californicus	*T. urticae* (R), E	10.9	59.2	14.1	7.2	4.3	3.0	Gotoh *et al*.(2004)
N. californicus	*T. urticae* (G), AS	10.6	71.4	20.7	6.7	4.8	3.9	Present study
A. cucumeris	*A. corpuzae*	-	-	20.0	-	-	7.7	Zhang *et al.* (2003)
A. fallacis	*T. urticae* (G)	11.2	74.2	19.7	8.2	5.6	3.9	Genini *et al*. (1991)
A. womersleyi	*T. urticae*, E	11.6	-	13.2	6.3	4.5	3.1	Lee & Ahn (2000)
A. womersleyi	*T. urticae* (R)	13.4	91.8	-	10.4	6.7	3.9	Kadono *et al*.(1975)
A. womersleyi	*T. kanzawai*	11.5	80.5	19.6	11.4	6.2	3.9	Nakagawa (1984)

[a]Developmental period from egg to adult emergence.
[b]*T.,Tetranychus; A.,Aponychus.* Mite species and stages provided: R, red form; G, green form; AS-all stages, E-egg.
[c] Estimated from original data.
t_o =lower temperature threshold.
K =thermal constant expressed in degree-days (DD).
Summary table was lifted and modified from Sabelis 1985b and Gotoh *et al*. 2004.

The total fecundity and average daily egg production of the Japanese *N. californicus* strain were lower than the report of Castagnoli & Simoni (1991) with the Italian strain and that of Gotoh *et al*. (2004) using the same strain. This might be brought about partially by differences in foods provided and local strains used. Gotoh *et al*. (2004) used solely a diet of eggs of the red form of *T. urticae* while the present study used composite stages of the green form of *T. urticae*, which was similar with that of Castagnoli & Simoni (1991) using all prey stages. There were many examples of phytoseiids showing different reproductive rates when fed with various preys (McMurtry & Rodriguez 1987) and different prey stages (Croft 1972; Sabelis 1985b; Bruce-Oliver & Hoy 1990; Castagnoli *et al*. 1999, 2004). Furthermore, female phytoseiid mites require multiple matings to attain their full reproductive potential, so the amount of sperm is critical in egg production (Amano & Chant 1977). In the present study, sample females were allowed to mate only once, which might suggest that the amount of sperm inseminated at the time of mating may not be enough resulting to low fecundity rate.

The intrinsic rate of natural increase (r_m) is one of the criteria that are extensively used in evaluating the efficacy of many predatory mites against spider mites (Tanigoshi 1982; Sabelis 1985b). At 25ºC, the r_m values obtained from the Italian and African strains of *N. californicus* fed with unspecified stages of *T. urticae* were close to that of the present study and higher than the Colombian strain (0.190; Mesa *et al*. 1990) (Table 8). Gotoh *et al*. (2004) reported an r_m value of 0.274 at 25ºC for the Japanese strain fed solely with eggs of *T. urticae* (red form). However, working with the same strain and temperature, the present study derived a lower r_m value of 0.206 when all stages of *T. urticae* (green form) were provided as preys. A part of this variation can be explained by different life stages of the prey offered to the predatory mites. When *Metaseiulus (=Typhlodromus) occidentalis* Nesbitt was fed with active stages of *T. pacificus* McGregor, its r_m value (0.207) was lower when fed with eggs (r_m = 0.244) (Bruce-Oliver & Hoy 1990). Similarly, the r_m values of *A. longispinosus* (Evans) were higher when fed with eggs than when fed with mobile stages of *T. urticae* (Kolodochka 1983, Lee & Ahn 2000). Therefore, the higher r_m values obtained by Gotoh *et al*. (2004) using the same strain could be expected with a diet of eggs alone. Also, the prey's host plant may affect r_m values. Castagnoli *et al*. (1999) reported a higher r_m value (0.274) with the Italian *A. californicus* strain fed with unspecified stages of *T. urticae* reared on strawberry leaves than those fed with the same prey species but reared on tomato leaves (r_m = 0.118). The present observation agrees with that of Gotoh *et al*. (2004) that in designing a biological control program using the Japanese *N. californicus* strain, it is important to know the diet and host plant histories.

The mean generation time (T) was greater when the Japanese *N. californicus* strain was fed with a combined diet of all stages (17.5 days) of *T. urticae* than those fed strictly on eggs (15.3 days) (Gotoh *et al*. 2004)(Table 8). But, the number of *N. californicus* female progeny produced per female (R_o) in each generation was greater on a diet of eggs alone (28.6)(Gotoh *et al*. 2004) than those produced per female feeding on a randomly mixed stages of *T. urticae* (22.92, Table 4 and 8). This smaller average in R_o reflected the greater mortality rate (lx) exhibited by *N. californicus* females fed with mobile juvenile stages of *T. urticae* as compared to a diet of non-mobile juvenile stage such as egg (Gotoh *et al*. 2004, Fig. 1 of present study). The R_o - and T-values of the Japanese strain in this study were comparable with those of the other foreign strains of *N. californicus.* Lee & Davis (1968), Laing (1969), Croft (1972) and Tanigoshi *et al*. (1975) reported varying R_o and r_m for *Metaseiulus occidentalis* fed with eggs or mixed stages of similar and different preys. Hence, interspecific and intraspecific variation in the population growth parameters can be expected when different prey stages were offered to predatory mites (Sabelis 1985b). These are critical information that should be considered in designing a biological control program involving *N. californicus.*

TABLE 8. Summary of life table parameters for some *Amblyseius* species at 25±2ºC.

Species	Prey[a]	R_o	r_m	T	Reference
Amblyseius bibens	*Tetranychus* AS	50.2	0.326	12.1	Blommers (1976)
Amblyseius californicus	*T. urticae* (G) E	29.1	0.287	11.7	Ma & Laing (1973)
Amblyseius californicus	*M. progresivus* AS	25.3	0.190	16.7	Mesa *et al*. (1990)
Amblyseius californicus	*T. urticae* (G) AS	29.9	0.190	17.4	Mesa *et al*. (1990)
Amblyseius californicus	*T. urticae* (G) AS	36.6	0.259	13.9	Castagnoli & Simoni (1991)
Amblyseius californicus	*T. urticae* (G) AS	11.2	0.227	11.6	Rencken & Pringle (1998)
Amblyseius californicus	*T. urticae* (G) AS	-	0.118	-	Castagnoli *et al*. (1999)
Amblyseius californicus	*T. urticae* (G) AS	-	0.274	-	Castagnoli *et al*. (1999)
Amblyseius californicus	*T. urticae* (R) E	28.6	0.274	15.3	Gotoh *et al.* (2004)
Neoseiulus californicus	*T. urticae* (G) AS	22.9	0.209	17.5	Present study
Amblyseius degenerans	*T. pacificus*	50.9	0.248	15.9	Takafuji & Chant (1976)
Amblyseius deleioni	*T. urticae* AS	24.9	0.286	11.2	Saito & Mori (1981)
Amblyseius eharai	*T. urticae* (G) AS	24.9	0.286	11.3	Saito & Mori (1981)
Amblyseius finlandicus	Pollen (*Typha* sp.)	32.0	0.232	20.3	Broufas & Koveos (2001)
Amblyseius longispinosus	*T. kanzawai* E	9.9	0.194	11.8	Shih & Shieh (1979)
Amblyseius longispinosus	*T. urticae* (G) N	10.3	0.273	8.5	Kolodochka (1983)
Amblyseius longispinosus	*T. urticae* (G) E	29.4	0.345	9.8	Kolodochka (1983)
Amblyseius orientalis	*P. ulmi* (+honey and pollen)	42.9	0.345	14.7	Xia *et al.* (1998)
Amblyseius paraki	*T. urticae* (G) AS	27.2	0.245	13.5	Saito & Mori (1981)
Amblyseius longispinosus	*T. urticae* (G) AS	32.2	0.333	10.4	Saito & Mori (1981)
Amblyseius womersleyi	*T. urticae* E	12.5	0.166	15.2	Lee & Ahn (2000)

[a]*T.,Tetranychus; M., Mononychellus; P., Panonychus.* Mite species and stages provided: R, red form; G., green form; AS- all stages, E- egg.
[b]*T. urticae* reared on tomato.
[c]*T. urticae* reared on strawberry.
Summary table was idea lifted and modified from Gotoh *et al*. 2004.

Some of the population parameters for *T. urticae* and some of its relative species are presented in Table 9. At 25°C, the r_m value (0.209) of the Japanese *N. californicus* strain was within the range of the r_m values of its *T. urticae* prey (0.128–0.259, Table 9). Since the speed of development was comparable between the prey and the predator, it appears that the ability of *N. californicus* may be poor when *T. urticae* population would be at peak. However, at higher temperature, its r_m value (0.285) was higher than its *T. urticae* prey, indicating its effectiveness on field horticultural crops during summer or in greenhouse crops where high temperature is usually maintained. However, in assessing the effectiveness of *N. californicus* as a biological control agent, aside from its capacity to increase, other factors like predation, searching ability and suitability of substrates should also be considered.

The sex ratio of phytoseiid mites is characterized by a female bias (Amano & Chant 1977; Tanigoshi 1982; Sabelis 1985a and b,). This was true with the Japanese *N. californicus* strain as well as with other *N. californicus* strains (Castagnoli & Simoni 1991; Rencken & Pringle 1998; Castagnoli *et al*. 1999, 2004; Gotoh *et al*. 2004; Toyoshima & Hinomoto 2004). Copulation duration, number of mating, and age of copulating males were just few of the factors studied and believed to

affect such high female percentage (El-Badry & Elbenhawy 1968; Schulten *et al*. 1978; Amano & Chant 1977). In the present study, sample females were mated only once while the counterpart strain used by Gotoh *et al*. (2004) were allowed to mate for 24h, and both studies yielded a high female progeny. In addition, it showed that temperature did not exert a critical effect on sex determination.

TABLE 9. Some reproductive parameters of some tetranychid species at 25±1ºC.

Species	Host plant	R_o	r_m	λ	
Tetranychus urticae	Red clover	65.0	0.259	1.295	Saito (1979)
	cotton cotyledons	74.8	0.219	1.245	Carey & Bradley (1982)
	Sirtaki gerbera	-	0.242	-	Krips *et al.* (1998)
T. urticae, green form	apple	17.42	0.187	-	Pringle *et al*. (1994)
T. urticae, carmine form	apple	7.84	0.128	-	Pringle *et al*. (1994)
T. pacificus	bush lima bean	108.3	0.290	1.340	Takafuji & Chant (1976)
	cotton cotyledons	44.6	0.207	1.229	Carey & Bradley (1982)
T. mcdanieli	bean	75.1	0.201	1.223	Tanigoshi *et al*. (1975)

[a]Summary table idea was lifted and modified from Sabelis 1985a and b.
R_o = net reproductive rate (per generation)
r_m = intrinsic rate of natural increase (per day)
λ = finite rate of increase (per day)

All stages of *T. urticae* were consumed by the Japanese *N. californicus* strain. As the density of juvenile prey increased, predation likewise increased. The same trend was observed with the same species fed with *T. cinnabarinus* (Boisduval) (Friese & Gilstrap 1982) or *Panonychus ulmi* Koch (Jolly 2000). Other predatory mites showed the same functional response (Shih *et al.* 1979; Kim *et al*. 1993; Zhang, Y.-X. *et al.* 1998; Castagnoli & Simoni 1999; Castagnoli *et al*. 1999b; Thongtab *et al.* 2001). Furthermore, the present results showed that *N. californicus* would prey more on juvenile stages than adult male or female stages of *T. urticae* in all situations when there were ample preys. This was similar with *T. bambusae* Ehara fed with *Schizotetranychus nanjingensis* Ma and Yuan (Zhang Y.-X. *et al.* 1999a). Oviposition of the Japanese *N. californicus* strain likewise increased when egg, larvae and nymph densities increased. This was true with other phytoseiid mites studied (Takafuji & Chant 1976; Sabelis & Jansen 1994; Zhang Y.-X. *et al.* 1999b; Walzer & Schausberger 1999a & b). However, if provided exclusively with adult male or female preys, oviposition of *N. californicus* remained low, even though a comparable number of this prey stage was consumed. Blommers *et al.* (1976 & 1977) suggested that spider mite adult male or female might constitute an inferior type of food. Furthermore, while the food value of different prey stages are important, it appears that the dietetic value of spider mite juvenile seems to equal that of eggs, since oviposition by the female predator was the same whether fed with prey eggs or mobile juveniles (Table 6 & Fig. 3; Blommers 1976 & 1977). Huffaker *et al.* (1970) considered it an advantage if a predator can survive and maintain its population at low prey density. The present study showed that the Japanese *N. californicus* strain could survive and reproduce at low prey density (about 5). Moreover, this strain can be considered effective against non-mobile and mobile juvenile stages of *T. urticae.* However, observation in the present study was limited to 7 days, hence observation longer than 7 days would further the present knowledge in *N. californicus* predation. Overall, the present study identified some characteristics listed by McMurtry (1982) for a predatory mite to be considered a successful biological control agent. The Japanese *N. californicus* strain has a short generation time, intermediate fecundity, r_m and R_o comparable with the other *Amblyseius* species important in biological control

programs. *N. californicus* seems better adapted to high temperatures and may be a good candidate for biological control of *T. urticae* attacking greenhouse and field horticultural crops. In addition, the present study showed that the performance of *N. californicus* was greatly affected by their food resources.

Acknowledgement

We are grateful to Drs. Keiji Takasu (Kyushu University) and Kaoru Maeto (Kobe University) for the statistical analyses; Ms. Y. Ishii (Chiba University) for sharing the techniques in mass rearing of mites; and to the Ministry of Education, Culture and Sports of the Government of Japan, for which without its financial support, this study has not been made possible.

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Accepted by Z.-Q. Zhang: 18 Aug. 2006